

USING LANDSCAPE-LEVEL DATA TO PREDICT THE DISTRIBUTION OF BIRDS ON A MANAGED FOREST: EFFECTS OF SCALE

MICHAEL S. MITCHELL,¹ RICHARD A. LANCIA,² AND JOHN A. GERWIN³

¹USGS, Alabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences, Auburn University, Auburn, Alabama 36849 USA

²Department of Forestry, North Carolina State University, Raleigh, North Carolina 27695-8002 USA

³North Carolina State Museum of Natural Sciences, Raleigh, North Carolina 27603 USA

Abstract. Selection of scale is critical when investigating ecological processes on landscapes because different patterns emerge in spatial data at different scales. Landscape studies commonly identify a single scale, or spatial extent of data, for assessing broad-scale habitat characteristics, without regard for the sensitivity of spatial data to the scale at which they are measured. An incorrect selection of scale can lead to misleading or erroneous inferences about how animals are associated with coarse-grained habitat characteristics. We developed and compared three statistical models for predicting presence of selected bird species inhabiting a managed forest in South Carolina: a model based only on microhabitat characteristics, a model based only on landscape characteristics (summary statistics of forest age and type calculated at different spatial scales) derived from GIS data, and a model that combined microhabitat and landscape characteristics. In general, landscape models (Somer's $D = 0.61 \pm 0.16$; mean ± 1 SD) worked as well as microhabitat models ($D = 0.61 \pm 0.14$), and combining the two types provided only a slight improvement in the explanatory ability of the models ($D = 0.62 \pm 0.18$). Models for Neotropical and short-distance migrants had the highest fit to field data, whereas models for resident species had relatively poor fit. We refined our landscape models according to known or hypothesized information from the literature to improve their generality, and we tested their ability to predict presence of the same species on a second, independent data set collected on a different managed forest nearby in South Carolina. In general, landscape models were able to predict the distribution of selected birds on the second forest well ($D = 0.46 \pm 0.32$), although overall model fit was somewhat lower than for the first forest ($D = 0.61 \pm 0.16$). Model fit was greatest for Neotropical and short-distance migrants, and poorest for residents. Model fit did not vary according to successional status, but did vary with habitat specialization; model fit was highest for habitat specialists and lowest for generalists. Our results suggest that, in general, coarse landscape characteristics are most important to migratory bird species that are limited in the number of habitats they can use for breeding. For species with adequate fit of landscape models, we assessed relationships between landscape scales associated with habitat variables within each model and ecological characteristics. Scale did not vary with migratory status, successional status, or habitat specialization and appears to be a function of the unique natural history of a species. Scale was correlated with hypothesized area sensitivities for some forest interior species, but not all; some early-successional species also appeared to be area sensitive. We conclude that no single scale is appropriate for assessing landscape associations across all bird species, or across general ecological guilds of species. Our modeling approach provides forest managers with a robust, biologically based approach to assessing the effects of forest management on birds across an entire landscape, using only GIS data.

Key words: GIS; habitat selection; landscape and microhabitat models; logistic regression; managed forest; migratory birds; scale effects; South Carolina.

INTRODUCTION

Selection of appropriate scale by researchers is critically important to the investigation of ecological processes (Levin 1992, May 1994). For landscape-level investigations, selection of scale (i.e., the spatial extent of landscape data) is the defining challenge because different patterns in data emerge at different spatial

scales (Golley 1989, Wiens 1989, Kareiva 1994, Bissonette 1997). Studies intended to correlate presence or abundance of animal populations with landscape-scale habitat characteristics are particularly vulnerable to incorrect selection of scale because habitat characteristics can vary widely with scale (Fig. 1). For example, if a species inhabiting hardwood forests in Fig. 1 responded to habitat characteristics at a scale of 491 ha, then researchers that evaluate habitat on a scale of 20 ha are likely to conclude either a nonexistent or erroneous association between that species and its hab-

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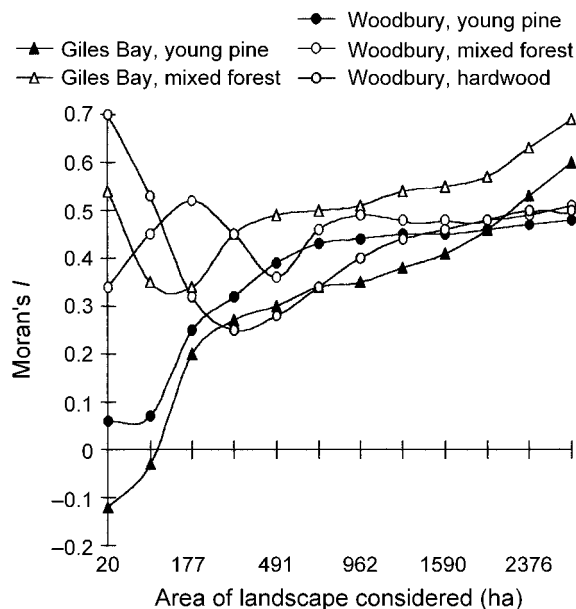


FIG. 1. Changes in a landscape metric (spatial continuity of forest age, indexed by Moran's I) with changes in scale of landscape sampled for three habitat types: young pine (0–5 yr old), mixed forest (>40 yr old), and hardwood forest (25–75 yr old) sampled at 235 locations on two tracts (Giles Bay and Woodbury) of a managed forest in South Carolina. The Giles Bay tract contained no hardwood forests. The figure illustrates scale sensitivity of landscape metrics; a metric can vary for a particular site across scales, or relative values of a metric for different sites can vary across scales. Selection of scale strongly influences both how a single site is described and how it compares to other sites.

itat (Orians and Wittenberger 1991). An incorrect choice of scale can lead to misleading insights into broad-scale processes, which can have undesired consequences if these form the basis for management or conservation policy. Nonetheless, many studies arbitrarily select scales used to define a landscape, ranging from 0.1 ha to >3000 ha (Wenny et al. 1993, Knick and Rotenberry 1995, McGarigal and McComb 1995, Bolger et al. 1997, Hagen et al. 1997, Rosenberg et al. 1999), without justification for the scale that was chosen. Few studies acknowledge the scale dependency of their data and evaluate landscapes on more than one scale (Robbins et al. 1989, Bissonette et al. 1997, Storch 1997, Turner et al. 1997, Saab 1999, Swindle et al. 1999).

In this paper, we present landscape models for predicting the presence of selected bird species and evaluating landscape scales relevant to birds. We developed and tested the models using data from two managed forests in South Carolina. Our work was part of a collaboration between private industry (International Paper Company, Westvaco Corporation, the National Council for Air and Stream Improvement), the Audubon Society, USDA Forest Service (Savannah River Ecology Laboratory), National Fish and Wildlife Foun-

dation, North Carolina State University, the North Carolina State Museum of Natural Sciences, Clemson University, and University of Georgia, whose joint objective was to develop a comprehensive model of forest management incorporating both ecological and economic considerations. The purpose of our research was to provide forest managers with broadly applicable, ecologically robust models that would allow them to evaluate the effects of forest management on forest birds in a comprehensive model of forest management. Our models were designed to (1) use landscape data readily available to managers of private forest lands, and (2) make robust, spatially informed predictions of presence for a diversity of bird species based on sound associations between landscape characteristics and known avian ecology. We emphasize at this point that our models were designed to predict a relatively coarse biological phenomenon (presence/absence) on a landscape scale, and were not intended to address abundance of birds, distributions of birds on fine geographic scales (i.e., stand level), or the long-term viability of bird populations on a managed forest.

To satisfy our first design consideration, we used only landscape data readily available to land managers through geographic information systems (GIS): forest age and forest type (dominant overstory species). This is based on the intuitive notion that suitable habitat for most forest bird species at its coarsest resolution can be defined using these two variables. Additionally, because the comprehensive model of forest management is computationally complex and represents an iterative approach to exploring management alternatives, we limited the metrics we used to assess landscapes to simple statistics (e.g., mean, standard deviation, spatial autocorrelation, percentage representation of classes) of the spatially distributed data for computational simplicity. Although many ways of measuring a landscape exist, by considering only the distributions of forest ages and types (characteristics with known associations with animals) within a defined area, our approach assumes less about how landscape characteristics might relate biologically to birds than would the use of more complex metrics.

To satisfy our second design consideration for our models, we needed to model accurately the relationships between presence of select bird species and the distribution of forest age and type classes on the landscape, at scales appropriate to each species. Coarse habitat associations are well documented for most forest birds in the eastern United States (Hamel et al. 1982). Although numerous studies have found a relationship between forest area and abundance or presence of birds (see Robbins et al. 1989 for a thorough review, but see also Villard 1998), and many species have been characterized as area-sensitive (Freemark and Collins 1992), little is known about what landscape scales are important to birds. Traditionally, studies of habitat associations have focused on a fine scale (e.g., micro-

TABLE 1. Species of forest birds, arranged according to migratory class, and the successional stage and number of potential breeding habitats for each, used to develop and test landscape models of presence on managed forests in South Carolina.

Species	Scientific name	Abbreviation†	Successional stage‡	No. potential breeding habitats§
Neotropical migrants				
Acadian Flycatcher	<i>Empidonax vireescens</i>	ACFL	2.50	8
American Redstart	<i>Setophaga ruticilla</i>	AMRE	2.50	5
Black-and-white Warbler	<i>Mniotilta varia</i>	BAWW	2.50	8
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	BGGN	2.75	11
Hooded Warbler	<i>Wilsonia citrina</i>	HOWA	2.75	10
Indigo Bunting	<i>Passerina cyanea</i>	INBU	1.00	13
Kentucky Warbler	<i>Oporornis formosus</i>	KEWA	3.00	7
Northern Parula	<i>Parula americana</i>	NOPA	2.75	10
Ovenbird	<i>Seiurus aurocapillus</i>	OVEN	2.75	8
Prairie Warbler	<i>Dendroica discolor</i>	PRAW	1.00	14
Prothonotary Warbler	<i>Protonotaria citrea</i>	PROW	2.50	5
Red-eyed Vireo	<i>Vireo olivaceus</i>	REVI	2.75	11
Swainson's Warbler	<i>Limnithlypis swainsonii</i>	SWWA	2.75	7
Wood Thrush	<i>Hylocichla mustelina</i>	WOTH	2.75	11
Yellow-breasted Chat	<i>Icteria virens</i>	YBCH	0.50	12
Short-distance migrants				
Common Yellowthroat	<i>Geothlypis trichas</i>	COYE	0.50	20
Pine Warbler	<i>Dendroica pinus</i>	PIWA	2.75	9
Residents				
Carolina Chickadee	<i>Poecile carolinensis</i>	CACH	2.75	18
Carolina Wren	<i>Thryothorus ludovicianus</i>	CARW	2.00	20
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO	2.75	20
Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA	2.00	20
Pileated Woodpecker	<i>Dryocopus pileatus</i>	PIWO	2.75	16
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	RBWO	2.75	17
Tufted Titmouse	<i>Baeolophus bicolor</i>	TUTI	2.75	17

† American Ornithologists' Union species abbreviations, used in subsequent tables and figures.

‡ Derived from Hamel et al.'s (1982) classification system for bird habitats: Hamel et al.'s grass-forb stage = 0, shrub-seedling stage = 1, sapling-poletimber stage = 2, and sawtimber stage = 3. Hamel et al.'s (1982) classification of bird species according to these classes was used to assign a successional stage to each species. Where Hamel et al. indicated a species could be present in more than one successional stage, the average stage value was assigned.

§ From Hamel et al. (1982: Appendix B).

habitat), whereas the processes underlying observed patterns (e.g., habitat selection, foraging and mating behaviors, source/sink dynamics) may actually take place on a much broader scale (Maurer and Villard 1994, Villard et al. 1995, Wiens 1995, Villard 1998). Several studies have evaluated relationships between birds and landscapes at arbitrarily chosen, fixed scales (Wenny et al. 1993, Knick and Rotenberry 1995, McGarigal and McComb 1995, Bolger et al. 1997, Hagen et al. 1997, Rosenberg et al. 1999). Robbins et al. (1989) showed, however, that presence of many forest birds had a nonlinear relationship with forest area across different scales, and that these relationships were species specific; these results suggest that an incorrect choice of scale for sampling could result in misleading predictions for any one species, and that no one scale of measurement would be sufficient for understanding broad-scale habitat relationships across multiple species. Because little is known about landscape scales governing habitat selection in birds, we wanted to avoid making a priori selections of scale that

could affect the accuracy of our models. Therefore, we evaluated patterns of bird presence and landscape characteristics across a spectrum of scales as part of our modeling process, in essence allowing the birds to tell us what scales were important to them.

We developed our landscape models by statistically associating bird and forest data collected on land owned by International Paper Company (Site 1) on the Coastal Plain of South Carolina. To evaluate how our landscape models compared to traditional modeling approaches, we developed microhabitat models using the same statistical approach. Because a complete habitat model for any species could include both microhabitat and landscape characteristics (Knick and Rotenberry 1995), we also developed combined microhabitat/landscape models for comparison. Because so little is known about scales at which birds select habitat, an exploratory statistical approach was necessary in the initial development of the models and was sufficient for contrasting alternative modeling approaches. Statistical models that are most parsimonious for the generating data set,

TABLE 2. Coarse habitat associations and hypothesized landscape scales important in determining presence for select bird species, taken from the literature (see *Method* and *Results* for citations).

Species†	Forest type	Forest age‡	Scale§	Relation-ship to dH ₂ O
Neotropical migrants				
ACFL	hardwood/mixed	sawtimber	fine, broad	–
AMRE	hardwood	sawtimber	broad	–
BAWW	hardwood/mixed	sawtimber	broad	–
BGGN	hardwood/mixed	pole/sawtimber	fine, medium	–
HOWA	hardwood/mixed	variable	medium, broad	–
INBU	variable	grass/seedling	fine	0
KEWA	hardwood	sawtimber	fine, medium	–
NOPA	variable	pole/sawtimber	medium, broad	–
OVEN	mixed	sawtimber	medium, broad	+
PRAW	pine	seedling	fine	0
PROW	hardwood	sawtimber	unknown	–
REVI	hardwood/mixed	pole/sawtimber	fine	0
SWWA	hardwood	mixed	unknown	–
WOTH	hardwood/mixed	pole/sawtimber	fine, medium	0
YBCH	variable	grass/seedling	unknown	0
Short-distance migrants				
COYE	variable	grass/seedling	fine	0
PIWA	pine	pole/sawtimber	unknown	0
Residents				
CACH	variable	pole/sawtimber	fine	0
CARW	variable	sapling-sawtimber	fine	0
DOWO	hardwood/mixed	pole/sawtimber	unknown	0
NOCA	variable	mixed	unknown	0
PIWO	hardwood/mixed	sawtimber	broad	–
RBWO	variable	pole/sawtimber	fine, medium	0
TUTI	hardwood/mixed	pole/sawtimber	fine, medium	0

† Species abbreviations are defined in Table 1.

‡ Forest age classes are from Hamel et al. (1982).

§ Multiple scales indicate contradictory information in literature.

|| Distance to water. A minus symbol indicates a decreasing probability of presence as distance from water increases.

however, may lack both biological information needed to test ecological hypotheses and the generality needed to have any predictive power for another data set (Burnham and Anderson 1998). Because it was our objective to use our models in both of these ways, we modified our statistical models based on known biological information for each bird species to create second-generation models. To evaluate the generality of these models, we tested their ability to explain the data on Site 1 (to determine if modifications strongly altered their performance), and we evaluated their ability to predict patterns in bird presence on a different managed forest owned by Westvaco Corporation (Site 2), also on the Coastal Plain of South Carolina.

Using only those landscape models that appeared robust across both sites, we evaluated variation in model fit and landscape scales important in predicting presence among different forest birds. To determine whether landscape characteristics might be more important to some species than others, we evaluated relationships between fit of landscape models and successional classes, migratory status, and habitat specialization of birds. To evaluate variation in scales of habitat selection among the different species, we looked for rela-

tionships between scale(s) and successional classes, migratory status, and habitat specialization of birds. We hypothesized (Freemark and Merriam 1986, Robbins et al. 1989, Flather and Sauer 1996) that:

1) mature forest birds would be associated with broader landscape scales than early-successional species,

2) Neotropical migrants would be associated with broader scales than short-distance migrants, which in turn would be associated with broader scales than year-round residents, and

3) habitat specialists would be associated with broader scales than generalists.

METHODS

Study areas

Site 1.—Site 1 comprised the Giles Bay and Woodbury tracts in Britton's Neck, South Carolina (33°52' N; 79°22' W), owned and managed by International Paper Company. The tracts are contiguous and lie on the peninsula formed by the confluence of the Great Pee Dee and Little Pee Dee Rivers, containing >8100 ha of planted loblolly pine (*Pinus taeda*) and longleaf

TABLE 3. Structure and fit of landscape, microhabitat, and combined microhabitat/landscape models generated by logistic regression to explain presence of select bird species on a managed forest in South Carolina.

Species	<i>n</i>	Microhabitat				Landscape				
		Slope	Variable	<i>C</i>	<i>D</i>	Slope	Variable	Scale	<i>C</i>	<i>D</i>
Neotropical migrants										
ACFL	104	+	overht	76.5	0.55	+	mean age	79	83.1	0.67
AMRE	32	+	overht	91.7	0.84	-	% pine	8	82.8	0.73
		-	vdl			-	% pine	8		
BAWW	3	+	pba	95.6	0.91
BGGN	114	+	vines	73.2	0.47	-	% pine	79	57.9	0.34
		+	pba			-	vdh			
HOWA	47	+	overht	78.1	0.57	-	% pine	491	81.1	0.62
		+	vines							
INBU	68	-	overht	80.3	0.61	-	mean age	8	88.0	0.76
KEWA	10	...	CC	+	SD age	20	79.2	0.60
NOPA	120	+	...	78.1	0.60	+	SD age	177	84.7	0.70
		-	overht			+	mean age	962		
OVEN	37	-	pba	77.9	0.63	-	MI age	314	86.9	0.74
		+	vines			+	% pine	2		
PRAW	58	-	pba	84.5	0.69	+	dH ₂ O	2827	82.2	0.65
		-	overht			+	MI type	20		
PROW	93	+	vines	86.7	0.74	+	mean age	8	94.2	0.89
		+	vdh			+	% pine	8		
REVI	78	-	overht	80.8	0.62	+	mean age	8	72.6	0.48
		+	midht			-	% pine	79		
SWWA	32	+	hwba	78.8	0.58	-	mean age	2	79.0	0.60
		+	pba			-	% pine	20		
WOTH	23	...	overht	+	% pine	1963	69.8	0.41
YBCH	39	-	hwba	85.3	0.71	+	MI age	314	93.3	0.87
		-	...			-	mean age	2		
Short-distance migrants										
COYE	69	+	vdl	84.7	0.70	+	% pine	2	67.0	0.51
		-	CC			-	mean age	1257		
PIWA	56	-	hwba	+	mean age	2376	85.6	0.72
		+	...			+	% pine	2		
Residents										
CACH	94	+	overht	71.9	0.44
CARW	196	-	vdl
				
DOWO	20
HAWO	4
NOCA	183	+	CC	62.5	0.37	-	MI age	1590	75.1	0.51
PIWO	75
RBWO	118	+	mean age	2827	68.2	0.37
TUTI	126

Notes: Model fit is indicated by percentage concordance (*C*; the number of times a bird was present and the probability of presence estimated by the model was greater than the probability of absence, divided by total observations) and Somer's *D* (*C* adjusted for the number of nonconcordant predictions, ranging from -1 to 1, indicating complete disagreement to complete agreement between predictions and observations); *n* = number of locations where the species was present. Age is forest age, spp. is overstory tree species, % pine is the proportion of pine in the overstory, MI is Moran's *I* statistic of spatial continuity (-1 = highly fragmented, 1 = homogenous), SD is standard deviation, scale refers to area (ha) of a circle centered on the sampling point in which the variable was measured, dH₂O is distance to nearest water, overht = overstory height, vines = number of vines, vdl = low vertical density, vdh = high vertical density, midht = midstory height, CC = canopy closure, hwba = hardwood basal area, pba = pine basal area, and snags = number of snags. Ellipses (...) indicate that no model was generated.

TABLE 3. Extended.

Slope	Variable	Combined		
		Scale	C	D
+	mean age	79	83.1	0.67
-	% pine	8		
-	% pine	8	82.8	0.73
...
-	% pine	79	57.9	0.34
+	vines		88.6	0.77
-	% pine	491		
+	SD age	20		
-	CC		85.2	0.71
-	mean age	8		
+	SD age	177	79.2	0.60
+	mean age	962	84.7	0.70
+	pba		86.2	0.73
+	dH ₂ O			
-	MI age	2		
-	overht		83.2	0.67
+	% pine	20		
+	mean age	8	94.2	0.89
-	% pine	79		
+	overht		80.8	0.62
-	vdl			
+	CC		90.6	0.81
-	mean age	2		
-	MI age	79		
-	% pine	20		
+	% pine	1963	69.8	0.41
-	overht		92.4	0.85
+	MI age	314		
-	mean age	1257		
-	CC		83.1	0.67
+	% pine	2		
+	mean age	2376	85.6	0.72
+	% pine	2		
-	vdh		62.1	0.25
...
...
...
...
-	MI age	1590	75.1	0.51
...
...
+	mean age	3000	68.2	0.37
...

pine (*P. palustris*), extensive bottomland hardwoods (bald cypress, *Taxodium distichum*; sweetgum, *Liquidambar styraciflua*; green ash, *Fraxinus pennsylvanica*; red maple, *Acer rubrum*; American sycamore, *Platanus occidentalis*; laurel oak, *Quercus hemisphaerica*), and Carolina Bays. Forest management techniques varied on the tracts, from intensive management (20-yr rotations, harvest by clearcutting followed by site prep-

aration) of pine plantations harvested on Giles Bay, to a variety of rotation lengths and harvesting techniques among the diverse forest types on Woodbury (Peters 1999).

Site 2.—Site 2 comprised the Ashley District, located ~135 km southwest of the Giles Bay and Woodbury tracts and 24 km west of Charleston, South Carolina (32°84' N; 80°42' W), owned and managed by Westvaco Corporation. The Ashley District is approximately 33 200 ha in size, primarily composed of stands of loblolly pine mixed with bottomland hardwood hummocks and gumponds (black gum, *Nyssa sylvatica*; bald cypress, *Taxodium distichum*; red maple, and green ash). Pine stands on the Ashley District were intensively managed on 20-yr rotations, hardwood stands were managed on ~60-yr rotations, and gum ponds were typically excluded from management. Timber was harvested on the Ashley District primarily by clearcutting, followed by site preparation on intensively managed stands (Turner 1998).

Bird, habitat, and landscape data

We used bird data collected using fixed-radius (50-m) point counts (Hutto et al. 1986) each breeding season at 235 locations on Site 1 in 1997 and 1998 (Peters 1999), and at 288 locations on Site 2 from 1996 to 1999 (Turner 1998; J. C. Turner, *unpublished data*). Sampling plots were distributed among forest types according to a stratified design, were no closer than 250 m from other plots, and most were 25 m from stand boundaries to ensure independence of samples and to minimize edge effects. Counts were taken each day from first light until 1000. Sampling was skipped on rainy days or when visibility was very low. Each sampling period at each plot lasted 5 min. All birds detected were recorded as either being within the 50-m plot, or outside. Flyovers were noted separately. A species was recorded as "present" at a plot if it was heard or observed within 50 m. See Peters (1999) and Turner (1998) for detailed results of sampling.

Two GIS layers, one depicting age, the other forest type of stands, were provided for each study site by International Paper Company and Westvaco Corporation. We converted the data to a raster format at a 50-m resolution (e.g., the dimension of each pixel was 50 × 50 m). Stand age was measured in years since last harvest or site preparation. GIS data for forest types from both companies were simplified into hardwood and pine overstory classes.

Microhabitat data were collected at 202 of the 235 bird sampling plots at Site 1 only. At the center of each plot, a spherical densiometer was used to measure percentage canopy closure, mean overstory and midstory height were measured with a clinometer, diameter at breast height was measured for the nearest 5 trees, and the number of snags within 50 m of each plot center was counted. Mean basal area was calculated for hardwoods and pines separately. Vertical density of vege-

tation was estimated using a 2.5-m coverboard at two heights: 0–1.5 m, low vertical density (vdl); 1.5–2.5 m, high vertical density (vdh). Indices for vine abundance (1 = low, through 5 = high) and presence of cane (*Arundinaria* spp.; 1 = present, 0 = absent) within 10 m of the center of each plot were estimated (Peters 1999).

Statistical models

We used stepwise logistic regression (SAS 1990) to develop statistical models for predicting the presence of selected species of birds on Site 1. Selected species belonged to one of three categories: Neotropical migrants, short-distance migrants, or residents (Table 1). Species of management or conservation interest were selected for the Neotropical migrants category, all short-distance migrants observed in the field were selected, resident species were subjectively selected to be a representative sample of nonmigratory forest birds. At the time of our study, landscape data for Site 1 were available for 1997 only. We assumed that no forestry activities substantively changed the landscape from 1997 to 1998 because on a 20-yr rotation in a completely regulated forest only 5% would be cut in a given year. We pooled observations of bird presence over 1997 and 1998 (e.g., if a bird was present at a site in either or both years it was counted as present for that site).

Stepwise logistic regression builds models by selecting subsets of explanatory variables that best explain a binary response variable (SAS 1990). For all models, we used presence/absence for a species across all sampled sites as the response variable. For microhabitat models, we used each of the sampled habitat characteristics as explanatory variables; we set the significance threshold for entry and retention in the model during the model-building process at $P = 0.01$.

Explanatory variables for landscape models were based on simple summary statistics of forest age and forest type calculated for areas of different size around each point sampled for birds. Our field sampling procedures assume that sampling points separated by 250 m are independent, implying that the territory of a nesting bird (those species in Table 1) observed at a sampling point was fully contained within a circular area with a 250-m radius (~20 ha). Within these areas, we measured landscape characteristics on a relatively fine grain using circular areas with 80-m (2 ha) and 160-m (8 ha) radii, centered on each bird sampling point. Beginning with areas defined by a 250-m radius (i.e., outside of territories), we measured landscape characteristics on a coarser grain, using circular areas with radii ranging from 250 m (20 ha) to 3000 m (2827 ha) at 250-m intervals, centered on each bird sampling point. For each landscape area at each sampling point, we calculated the mean, standard deviation, and spatial continuity (indexed using the Moran's I statistic; Cliff and Ord 1981) of pixels contained within the area for

forest age. We also calculated Moran's I and percentage of pine for forest type for each landscape area. Moran's I is an index of autocorrelation among spatially distributed data, ranging between -1 (no continuity among values of neighboring data points, e.g., a forest with a highly disjunct spatial distribution of age classes) and 1 (complete continuity, e.g., a forest consisting of a single age class). Thus, for our models, a positive correlation between presence of a bird and Moran's I for forest age indicated an affinity of that species for a spatially homogeneous distribution of age classes; a negative correlation indicated affinity for a heterogeneous mix of age classes.

We also used Idrisi GIS (Eastman 1997) to calculate distance to nearest water for each sampling point and included this measure as an explanatory variable. Thus, for each point, 73 explanatory landscape variables were calculated (i.e., 5 landscape metrics measured at each of 12 scales, plus distance to water). None of these variables could be eliminated a priori from the analyses because so little is known about appropriate scales for assessing landscapes. Therefore, we set a conservative significance threshold of $P = 0.001$ for entry and retention in the logistic models to reduce the chance of spurious significance. For the 73 variables evaluated in each of the 24 models we generated, a P value of 0.001 yielded a probability that <2 of the 1752 variable evaluations resulted in spurious variable inclusion or exclusion in the models, which we deemed an acceptable risk. By definition, observations for a landscape characteristic across multiple scales are not independent of each other for any given location, but are not necessarily correlated between locations. Because we did not want to make a priori decisions about appropriate scales, we did not control for this correlation within explanatory landscape variables in our models.

For our combined microhabitat/landscape models, we used both microhabitat and landscape models with a significance threshold of $P = 0.001$. We assessed the explanatory power of all models using percentage concordance, C :

$$C = (nc + 0.5(t - nc - nd))/t$$

where t = the total number of field observations paired with model predictions, nc = the number of pairs that were concordant (i.e., a bird was observed at a location where the model predicted probability of presence), nd = the number of pairs that were discordant, and $t - nc - nd$ of the pairs were tied (SAS 1990). We also assessed model fit using a more stringent statistic, Somer's D :

$$D = (nc - nd)/t$$

which penalizes model performance for incorrect predictions, and ranges from -1 to 1 (indicating complete disagreement to complete agreement between predictions and observations). We qualitatively compared model fit for all species across the microhabitat, land-

scape, and combined microhabitat/landscape models to evaluate their relative explanatory power.

Second-generation models

To assess landscape-level habitat associations for each species, we compared the results of our statistical, landscape models to hypotheses about landscape characteristics drawn from the literature (Hamel et al. 1982, Freemark and Merriam 1986, Robbins et al. 1989, DeGraff and Rappole 1995, Flather and Sauer 1996, Kilgo et al. 1998; Table 2). Based on these comparisons, we modified our models for each species to increase their generality. We were conservative in our modifications, retaining insights on scale generated from the original models as much as possible and adding variables only where strong biological justification was present. We used logistic regression to construct a second set of exploratory models of presence for birds at Site 1, using a liberal significance threshold ($P = 0.50$) for variable entry and retention in the model. We ranked the resulting explanatory values according to the significance of their individual contribution to the strength of the exploratory model (P value based on Wald chi-square; SAS 1990). We then generated second-generation models by adding high-ranking landscape variables from the exploratory models to the first-generation models when they represented biological information (Table 2) otherwise absent in the first-generation models. Where no first-generation models were generated for a species, we generated second-generation models by selecting high-ranking variables from the exploratory models based solely on information in Table 2. Where biological information suggested distance to water should be a strong determinant of habitat suitability for a species (Table 2), we included this variable in the model, regardless of its relative ranking. To determine if our modifications strongly affected their ability to explain the data used to generate them, we tested these second-generation models using the data from Site 1.

Evaluation of second-generation models

We applied our second-generation models to data collected at Site 2 to determine their ability to predict patterns in an independent data set. We analyzed qualitatively the relative performance of the models on the two data sets, as well as patterns in model performance in the Site 2 data across the different bird species.

We based all of the following analyses of landscape associations for birds on only the second-generation models that had some predictive power for birds at Site 2 ($D \geq 0.20$). To determine whether the ability of landscape parameters to predict presence varied according to migratory status, we used analysis of variance (ANOVA; PROC GLM; SAS 1990) to compare mean model fit (average D between Sites 1 and 2) across migratory classes (Table 1). We defined a continuum of successional specialty based on Hamel et al.'s (1982) clas-

sification system for bird habitats, identifying Hamel et al.'s (1982) grass-forb stage as 0, his shrub-seedling stage as 1, his sapling-poletimber stage as 2, and his sawtimber stage as 3. We used Hamel et al.'s (1982) classification of bird species according to these classes to assign a successional stage to each of our species (Table 1). Where Hamel et al. (1982) indicated a species could be present in more than one successional stage, we assigned the average stage value to that species. Hamel et al. (1982: Appendix B) also identified the number of habitats in which different species can successfully breed. To evaluate whether the ability of landscape parameters to predict presence varied according to degree of habitat specialization or successional specialty, we evaluated across all species the relationship between model fit and the number of potential breeding habitats (Table 1) for each species and successional stage (PROC REG; SAS 1990). To determine whether scale of habitat selection for a species indicated by our landscape models might be a trait shared among members of ecological guilds of birds, we evaluated across all species the relationships between migratory status (PROC GLM; SAS 1990), successional specialty, or degree of habitat specialization (PROC REG; SAS 1990), and the mean scale (i.e., mean spatial extent of landscape variables) of landscape variables in the logistic regression model for each species.

RESULTS

Statistical models

Logistic regression generated microhabitat, landscape, and combined microhabitat/landscape models for all species at the threshold of acceptance we set ($P = 0.001$), with several exceptions. Only a microhabitat model was generated for the Black-and-white Warbler, no microhabitat model was generated for the Kentucky Warbler, Wood Thrush, or Red-bellied Woodpecker, no landscape model was generated for the Carolina Chickadee, and no models at all were generated for the Carolina Wren, Downy Woodpecker, Pileated Woodpecker, or Tufted Titmouse (Table 3). Model fit tended to be poor for species that were present either at very few ($n < 20$) or very many ($n > 100$) sampling points (Table 3; Fig. 2).

Generally, landscape models ($D = 0.61 \pm 0.16$; mean ± 1 SD) fit the data as well as microhabitat models ($D = 0.61 \pm 0.14$), with the exception of the American Redstart, Blue-gray Gnatcatcher, Red-eyed Vireo, and Common Yellowthroat (Table 3; Fig. 2). Combined microhabitat/landscape models ($D = 0.62 \pm 0.18$) fit only slightly better than microhabitat and landscape models; microhabitat models fit better than combined models only for the American Redstart, Blue-gray Gnatcatcher, Prairie Warbler, Common Yellowthroat and Carolina Chickadee, landscape models fit better than combined models only for the Indigo Bunting, the Ovenbird, and

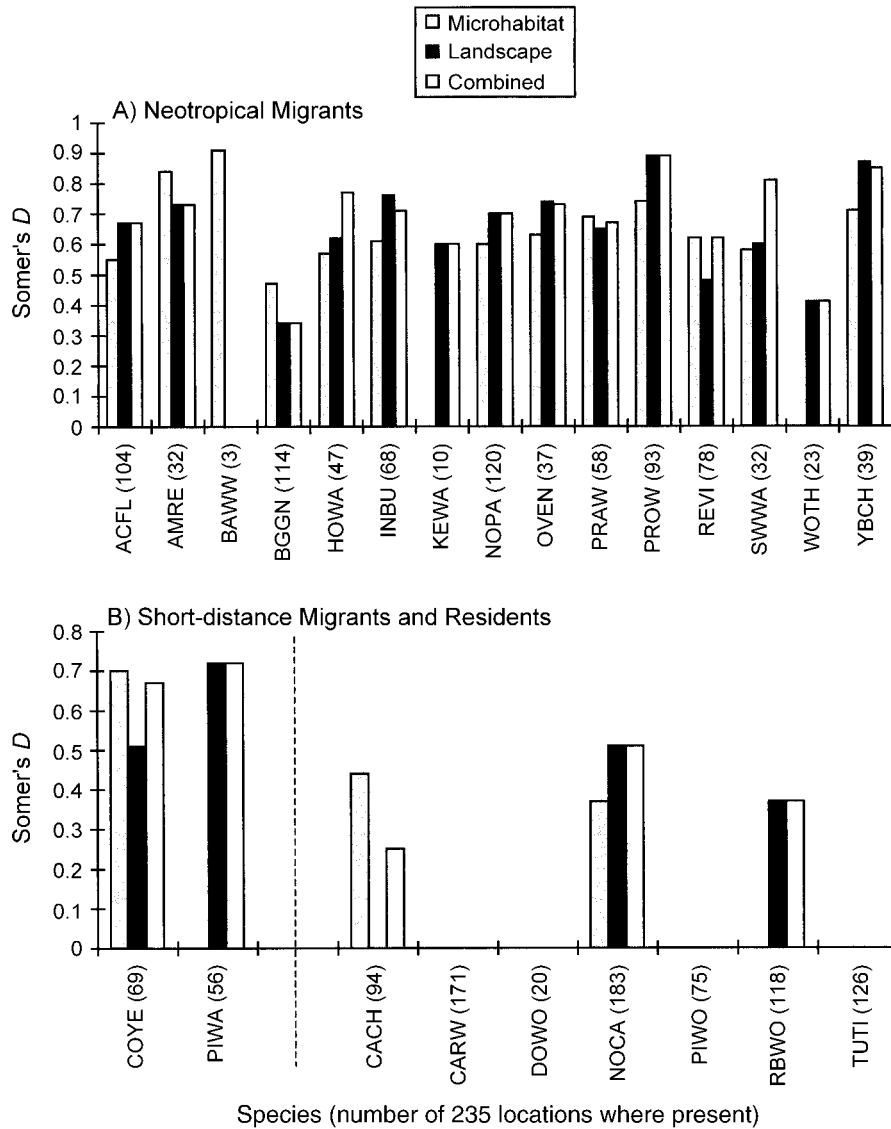


FIG. 2. Fit (Somer's D , ranging from -1 to 1 , indicating complete disagreement to complete agreement between predictions and observations) of microhabitat, landscape, and combined microhabitat/landscape models generated by logistic regression to explain presence of selected bird species on a managed forest in South Carolina. Panel (A) shows fit of models generated for Neotropical migrants; panel (B) shows fit of models generated for short-distance migrants and year-round residents (separated by dotted line). Missing information on model fit indicates that no statistically significant model was generated. See Table 1 for species abbreviations.

Yellow-breasted Chat (Table 3; Fig. 2). In some cases, combined models performed as well or better than both microhabitat and landscape models, suggesting important habitat information is contained in both kinds of data for select species (Hooded Warbler, Swainson's Warbler; Table 3; Fig. 2). Explanatory variables in combined models did not differ from those in microhabitat models for the Blue-gray Gnatcatcher, and Red-eyed Vireo, nor from those in landscape models for the Acadian Flycatcher, American Redstart, Kentucky Warbler, Northern Parula, Prothonotary Warbler, Pine Warbler, Northern Cardinal, and Red-bellied Woodpecker (Table 3).

Explanatory variables (without regard for scale) selected for all models and their relationships to presence for each species did not differ qualitatively from those predicted in Table 2, except that distance to water was included only in the model for the Ovenbird, the only species predicted to prefer upland habitats (Table 3). Because of the location of Site 1 in the swampy confluence of two rivers, the absence of distance to water in the models of those species predicted to prefer habitats near water might indicate the ubiquity of water on the site, rather than a lack of relationship between the birds and water. Models commonly did not include variables for both forest age and type.

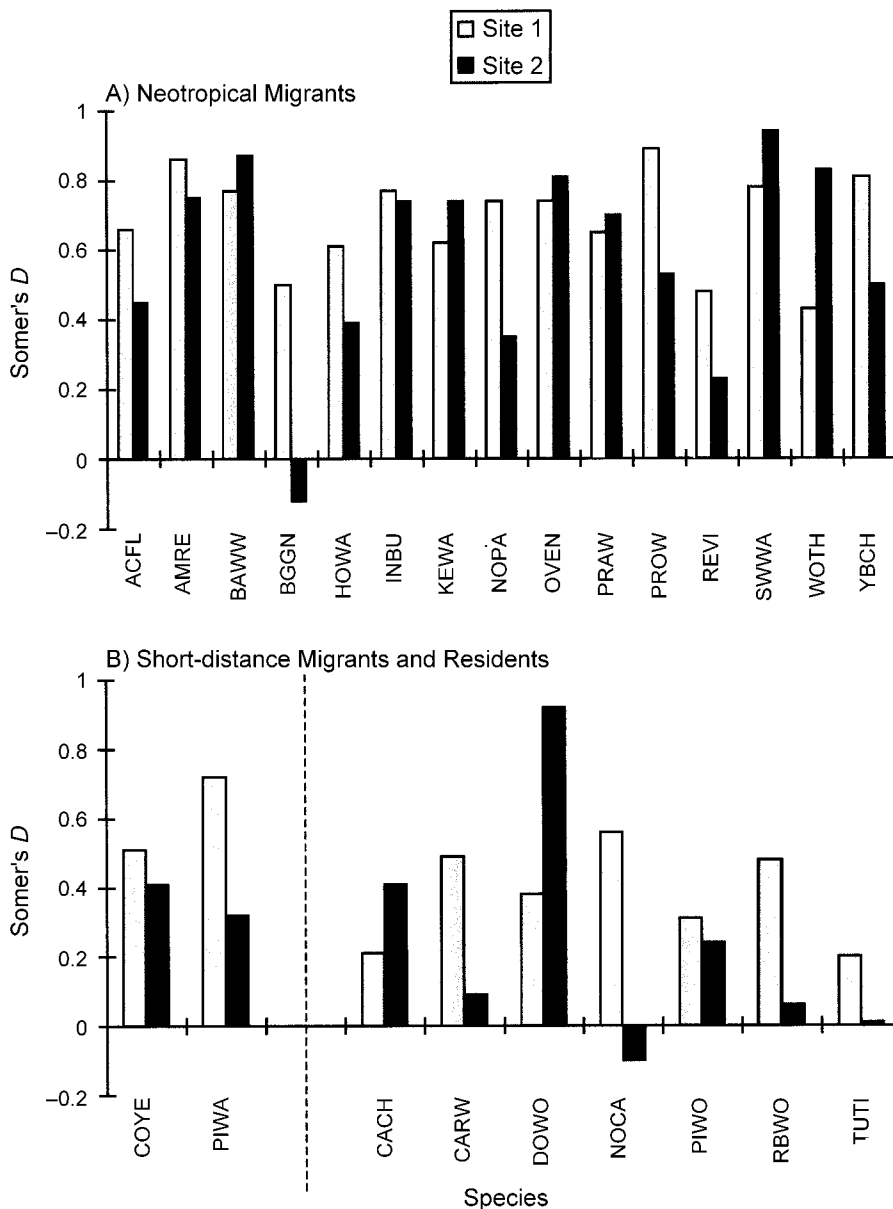


FIG. 3. Fit (Somers's *D*, ranging from -1 to 1, indicating complete disagreement to complete agreement between predictions and observations) of landscape models for predicting presence of selected bird species on two managed forests in South Carolina (Sites 1 and 2). Bird and landscape data from Site 1 were used to develop the landscape models using logistic regression, which were then tested for their ability to predict presence of birds at Site 2. Panel (A) shows fit of models generated for Neotropical migrants; panel (B) shows fit of models generated for short-distance migrants and year-round residents (separated by dashed line). See Table 1 for species abbreviations.

Second-generation models

We modified first-generation models for all species except for the Prairie Warbler, the Ovenbird, the Pine Warbler, and the Wood Thrush (Table 4), species for which no high-ranking explanatory variables from the exploratory logistic regressions matched missing biological information. Distance to water was added as an explanatory variable to the models of 11 species (Acadian Flycatcher, American Redstart, Black-and-white

Warbler, Blue-gray Gnatcatcher, Hooded Warbler, Kentucky Warbler, Northern Parula, Ovenbird, Prothonotary Warbler, Swainson's Warbler, and Pileated Woodpecker), and was the sole modification for three of these (Acadian Flycatcher, Hooded Warbler, and Kentucky Warbler; Table 4). Models were estimated based only on information in Table 2 for six species (Black-and-white Warbler, Carolina Chickadee, Carolina Wren, Downy Woodpecker, Pileated Woodpecker, and Tufted

TABLE 4. Structure and fit of first- and second-generation landscape models for select forest bird species on two managed forests in South Carolina (Sites 1 and 2).

Species	First-generation models					
	Slope	Variable	Scale	Site 1		
				<i>n</i>	<i>C</i>	<i>D</i>
Neotropical migrants						
ACFL	+	mean age	79	103	83.1	0.67
	-	% pine	8			
AMRE	-	% pine	8	32	82.8	0.73
BAWW	3
BGGN	-	% pine	79	114	57.9	0.34
HOWA	-	% pine	491	47	81.1	0.62
INBU	-	mean age	8	68	88.0	0.76
	+	SD age	20			
KEWA	+	SD age	177	10	79.2	0.60
NOPA	+	mean age	962	120	84.7	0.70
OVEN	-	MI age	314	37	86.9	0.74
	+	% pine	2			
PRAW	+	dH ₂ O	2827	58	82.2	0.65
	+	MI type	20			
	-	mean age	20	93	94.2	0.89
	+	% pine	8			
PROW	+	mean age	8	93	94.2	0.89
	-	% pine	79			
REVI	+	mean age	8	78	72.6	0.48
SWWA	-	mean age	2	32	79.0	0.60
	-	% pine	20			
WOTH	+	% pine	1963	23	69.4	0.43
YBCH	+	MI age	314	39	93.3	0.87
	-	mean age	2			
	-	mean age	1257			
Short-distance migrants						
COYE	+	% pine	2	65	67.0	0.51
PIWA	+	mean age	2376	56	85.6	0.72
	+	% pine	2			
Residents						
CACH	94
CARW	197
DOWO	20
NOCA	-	MI age	1590	181	75.1	0.51

TABLE 4. Extended.

Second-generation models								
Slope	Variable	Scale	Site 1			Site 2		
			<i>n</i>	<i>C</i>	<i>D</i>	<i>n</i>	<i>C</i>	<i>D</i>
+	mean age	79	103	83.1	0.66	331	72.2	0.45
-	% pine	8						
-	dH ₂ O							
-	% pine	8	32	92.7	0.86	3	87.2	0.75
+	MI spp.	491						
-	dH ₂ O							
+	mean age	1964	3	88.1	0.77	20	93.6	0.87
-	mean spp.	177						
-	dH ₂ O							
-	MI spp.	2827	114	74.8	0.50	310	44.2	-0.12
+	% pine	314						
+	SD age	2						
-	dH ₂ O							
-	% pine	491	47	80.1	0.61	281	69.3	0.39
-	dH ₂ O							
-	mean age	8	68	88.0	0.77	101	83.7	0.74
+	SD age	20						
+	mean age	2						
+	SD age	177	10	80.1	0.62	136	86.8	0.74
-	dH ₂ O							
+	mean age	962	120	86.9	0.74	272	67.3	0.35
-	% pine	20						
-	dH ₂ O							
...	89	90.5	0.81
...	146	85.1	0.70
+	MI spp	20	93	94.6	0.89	94	76.4	0.53
-	% pine	79						
+	SD age	2						
+	mean age	8						
+	dH ₂ O							
+	mean age	8	78	78.8	0.58	451	61.7	0.23
-	mean age	2376						
-	% pine	20						
-	MI age	20	32	88.9	0.78	20	96.7	0.94
+	MI age	491						
-	mean age	2						
+	mean age	2827						
-	MI spp.	2827						
-	dH ₂ O							
...	87	91.4	0.83
+	SD age	1257	39	90.0	0.81	300	75.0	0.50
-	mean age	2						
+	% pine	707						
-	mean spp.	2	65	69.4	0.48	260	70.5	0.41
+	% pine	2						
...	355	0.66	0.32
-	% pine	177	94	59.2	0.21	116	71.4	0.41
-	MI spp.	20						
+	SD age	79	197	74.4	0.49	567	0.54	0.09
-	mean age	79						
-	MI age	962						
+	mean age	79	20	68.3	0.38	39	96.0	0.92
-	MI spp.	2827						
-	MI age	1590	181	77.4	0.56	471	45.2	-0.10
+	MI spp.	707						

TABLE 4. Continued.

Species	First-generation models					
	Slope	Variable	Scale	Site 1		
				<i>n</i>	<i>C</i>	<i>D</i>
PIWO	75
RBWO	+	mean age	2827	118	68.2	0.37
TUTI	126

Notes: First-generation models were developed using logistic regression on data collected on Site 1 and were modified to incorporate known biological characteristics. Second-generation models were tested on Site 1 to evaluate the effects of model modification, and then tested on Site 2 to determine their ability to predict presence of birds on a different landscape. Model fit is indicated by percentage concordance (*C*; the number of times a bird was present and the probability of presence estimated by the model was greater than the probability of absence, divided by total observations) and Somer's *D* (*C* adjusted for the number of nonconcordant predictions, ranging from -1 to 1, indicating complete disagreement to complete agreement between predictions and observations); *n* = number of locations where species was present. Age is forest age, spp. is overstory tree species, % pine is the proportion of pine in the overstory, MI is Moran's *I* statistic of spatial continuity (-1 = highly fragmented, 1 = homogenous, e.g., MI spp. indicates fragmentation in the distribution of overstory tree species), SD is standard deviation, scale is area (ha) of a circle centered on the sampling point in which the variable was measured, dH₂O is distance to nearest water, overht = overstory height, vines = number of vines, vdl = low vertical density, vdh = high vertical density, midht = midstory height, CC = canopy closure, hwba = hardwood basal area, pba = pine basal area, and snags = number of snags. Ellipses (...) indicate that no model was generated.

Titmouse) for which no significant statistical models were generated (Table 4). All other modifications were the product of adding biologically important variables that ranked high in the exploratory regressions (American Redstart, Blue-gray Gnatcatcher, Indigo Bunting, Northern Parula, Prothonotary Warbler, Red-eyed Vireo, Swainson's Warbler, Yellow-breasted Chat, Common Yellowthroat, Northern Cardinal, and Red-bellied Woodpecker), or removing redundant variables (Table 4). Model modifications did not change the ability of models to explain presence of bird species on Site 1;

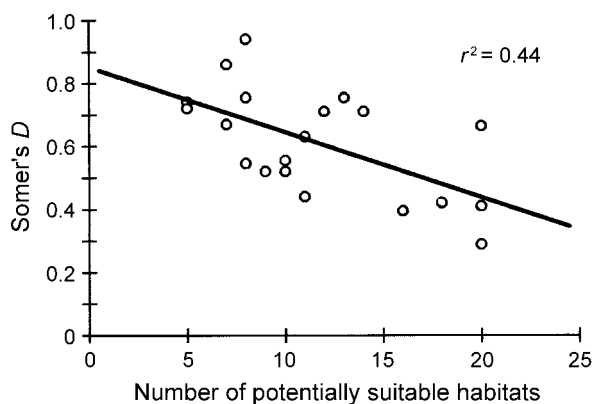


FIG. 4. Relationship of fit (Somer's *D*, ranging from -1 to 1, indicating complete disagreement to complete agreement between predictions and observations) of landscape models for explaining the presence of 24 forest birds on a managed forest in South Carolina to the degree of habitat specialization (indexed by the number of potentially suitable breeding habitats identified by Hamel et al. [1982] for each species).

mean *D* for both statistical and second-generation models was 0.61 ± 0.16 .

Test of second-generation models

In general, second-generation models were able to predict the presence of birds at Site 2 reasonably well; average model fit at Site 2 was 0.46 ± 0.32 , which, predictably, was not as high as it was for Site 1 (0.61 ± 0.16). Model effectiveness varied among species at Site 2. Models had strong predictive power for several species at Site 2, with model fit exceeding that for Site 1 (Black-and-white Warbler, Kentucky Warbler, Ovenbird, Prairie Warbler, Swainson's Warbler, Wood Thrush, Carolina Chickadee, Downy Woodpecker; Table 4, Fig. 3). Models for several species had model fit at Site 2 below that observed at Site 1 (Acadian Flycatcher, American Redstart, Blue-gray Gnatcatcher, Hooded Warbler, Northern Parula, Prothonotary Warbler, Red-eyed Vireo, Yellow-breasted Chat, Common Yellowthroat, Pine Warbler, Carolina Wren, Northern Cardinal, Red-bellied Woodpecker, and Tufted Titmouse); predictive power of the models was poor ($D \leq 0.20$) for some of these species (Blue-gray Gnatcatcher, Carolina Wren, Northern Cardinal, Tufted Titmouse; Table 4; Fig. 3), and they were excluded from further analyses (Table 4, Fig. 3).

Mean fit of second-generation models (average *D* between sites 1 and 2) differed among migratory classes of birds ($F = 8.45$, $df = 2, 21$, $P = 0.002$). Mean *D* for Neotropical migrants (0.62 ± 0.18) did not differ from that for short-distance migrants (0.48 ± 0.05), both of which differed from mean *D* for residents (0.30 ± 0.17 ; $P = 0.0020$). Mean *D* did not differ among

TABLE 4. Extended, continued.

Second-generation models								
Slope	Variable	Scale	Site 1			Site 2		
			<i>n</i>	<i>C</i>	<i>D</i>	<i>n</i>	<i>C</i>	<i>D</i>
+	MI age	79	75	65.1	0.31	220	62.0	0.24
-	MI age	314						
+	% pine	1257						
-	dH ₂ O							
+	mean age	2827	118	73.7	0.48	369	52.7	0.06
+	SD age	79						
+	% pine	177	126	59.6	0.20	530	50.5	0.01
-	MI spp.	20						
+	mean age	79						

successional stages of birds ($F = 2.03$, $df = 5, 18$, $P = 0.1229$) but was related to degree of habitat specialization; mean D was negatively correlated (slope = -0.03 , $r^2 = 0.44$, $P = 0.0004$) with the number of potential breeding habitats a species could use (Fig. 4).

Our second-generation models provided insights into landscape scales at which birds select habitat. Several species, such as the Hooded Warbler, appeared to associate with habitat on a single landscape scale (Table 4). Others, such as the Ovenbird and Prairie Warbler, appeared to respond to habitat on more than one scale (Table 4). For species with multiscale models, scales could either be consistent (e.g., 8 and 20 ha for Indigo Bunting) or quite different (e.g., 315, 2, and 1257 ha for the Yellow-breasted Chat; Table 4). Further, the relationship a species had with a habitat variable could

be different at different scales (e.g., the Swainson's Warbler was negatively associated with forest age and spatial continuity of age on fine scales, positively associated with them on broader scales; Table 4). Mean scale (i.e., mean spatial extent of landscape variables) of landscape variables among species (Fig. 5) was unrelated to successional stages ($P = 0.4283$), and did not vary across migratory classes ($F = 0.60$, $df = 2, 16$, $P = 0.5597$). Mean scale was also unrelated to degree of habitat specialization ($P = 0.8310$).

DISCUSSION

Our landscape models, incorporating appropriate scales, worked as well or better than traditional microhabitat approaches in predicting presence of forest birds. In only a few cases did our statistical landscape

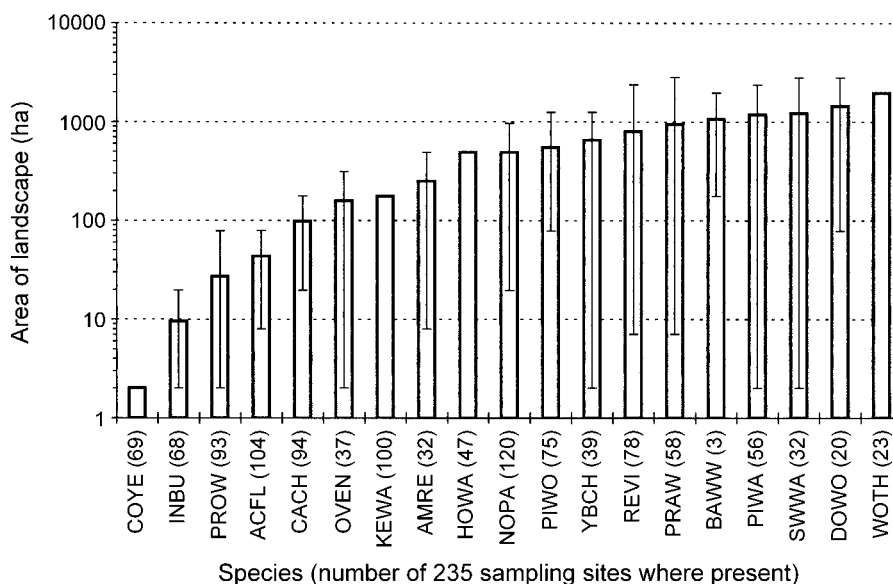


FIG. 5. Mean scale of landscape variables used for predicting the presence of select forest birds living on managed forests in South Carolina. Scales (note logarithmic divisions) were associated with each forest age and type variables of landscape models developed for each species on one managed forest and tested on another. Only models with good predictive power (Somers' $D > 0.25$) on the second managed forest are shown. Bars indicate mean scale; error bars indicate range of scales for species whose model contained more than one landscape variable. See Table 1 for species abbreviations.

models perform more poorly than microhabitat models. The overriding importance of landscape characteristics appears to be reinforced by the relatively low improvement of combined microhabitat/landscape models over landscape models, as well as the relative rarity of microhabitat variables included in the combined models. Our results agree with findings of Bolger et al. (1997) and Saab (1999) that landscape patterns can be a primary influence on distribution and occurrence of forest birds.

Our work has important implications for forest managers. First, using landscape data to predict distributions of birds on a managed forest is an attractive alternative to using microhabitat data, which requires intensive field sampling and can be difficult to model spatially for an entire forest. By contrast, simple, spatially explicit data on forest structure and composition are readily available in GIS databases. Our models show that these alone can be sufficient to model the distribution of birds on a landscape, with at least as much accuracy as other approaches we evaluated. Because data for forest age and type are spatially explicit, our approach provides managers with the ability to estimate the distribution of a given bird over an entire forest, with results displayed as a predictive surface (Fig. 6). This ability to visualize the distribution of a bird on a landscape is appealing, and alone can lead to management and conservation insights. On a more quantitative level, predictive surfaces can be generated for any distribution of forest ages and types, allowing planners to compare, on landscape scales, the effects on birds of alternative management scenarios prior to implementation. Finally, we demonstrated that landscape models can be sufficiently general to apply to different locations with similar habitats where the same species of birds are found. In addition to facilitating regional forest management, this generality suggests that an important aspect of the ecology of forest birds is captured by landscape models, offering some assurance to forest planners that model predictions will provide a reliable basis for management actions.

We reiterate an important qualification, however, to the application of our approach in forest planning. Our landscape models predicted only presence/absence on a landscape scale, which is a very coarse standard in ecological terms. Average success of simple models in predicting a binomial distribution does not compare with the complex reality of ensuring persistent populations of forest birds; we do not assume that the presence of a species in a given forest is sufficient to conclude that it is a member of a healthy breeding population with strong prospects for persistence. Our approach offers a biologically based, coarse-grained, landscape-scale starting point for evaluating the effects of forest management on the distribution of forest birds, and is not sufficient for predicting population dynamics on finer grained scales.

Performance of the landscape models provided some

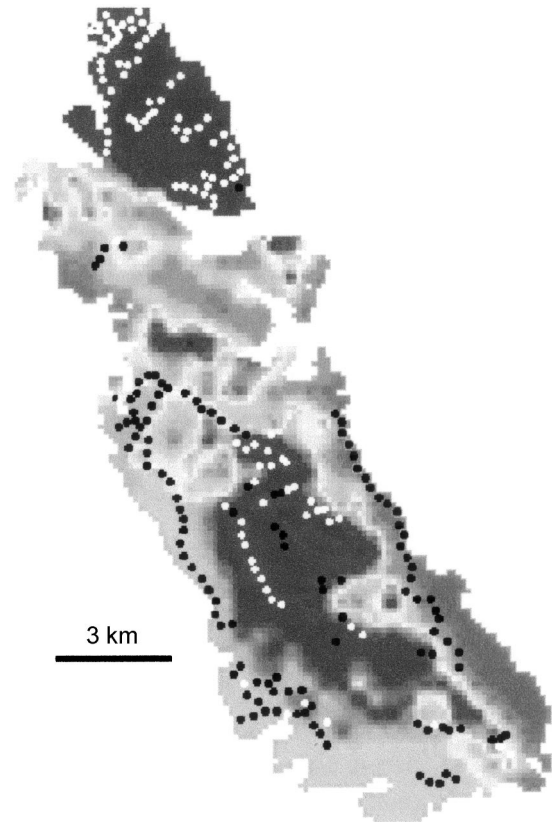


FIG. 6. Probability of presence predicted by statistical landscape model for the Prothonotary Warbler on a managed forest in South Carolina (Giles Bay and Woodbury tracts, International Paper, Incorporated). Logistic regression was used to model the presence of Prothonotary Warblers based on GIS data on forest age and type measured on multiple scales. Predicted probability of presence is high for light shades of gray, and low for dark shades of gray. Dots show the locations of 235 sites sampled for birds in 1996 and 1997: solid dots indicate Prothonotary Warblers were present; open dots indicate they were absent. Model fit was strong, with percentage concordance of predictions with observations, C , equal to 94% (Somers' $D = 0.89$).

interesting insights into the importance of landscape characteristics for different birds. Our models agree with the findings of Flather and Sauer (1996) that resident species were relatively insensitive to landscape characteristics, whereas the presence of migratory birds (either Neotropical or short-distance) strongly depended on them. Interestingly, our landscape models worked equally well across the successional continuum, implying that landscape characteristics are equally important to both mature forest specialists and pioneering opportunists. The strongest pattern we observed was the relationship between model fit and habitat specialization. Generalists were relatively insensitive to landscape characteristics, whereas specialists appeared to respond to them strongly. This pattern was not an artifact of the number of times the birds were observed (e.g., where statistical models fit both rare and ubiq-

uitous species poorly); fit of second-generation models estimated only from information in Table 2 was high for rare species and low for ubiquitous species (Table 4). Our results suggest that, in general, coarse landscape characteristics are most important to migratory bird species that are limited in the number of habitats they can use for breeding.

Our models provided insight into landscape scales at which birds select habitat. Scales suggested by our models agreed with hypothesized or commonly accepted scales (Table 2) for most of the species we modeled, although there were notable exceptions. In accordance with the insights of other researchers (Hamel et al. 1982, Freemark and Merriam 1986, Robbins et al. 1989, DeGraff and Rappole 1995, Flather and Sauer 1996, Kilgo et al. 1998), we found that Pileated Woodpeckers, Downy Woodpeckers, and Black-and-white Warblers appear to select habitat on relatively broad scales; American Redstarts, Hooded Warblers, Kentucky Warblers, Northern Parulas, and Ovenbirds appeared to select habitat on more moderate scales; and Carolina Chickadees, Indigo Buntings, and Common Yellowthroats appeared to select habitat on finer scales. Some of our findings disagreed with scales suggested by other researchers: Prairie Warblers (see Hamel et al. 1982), Red-eyed Vireos (see Robbins et al. 1989, Kilgo et al. 1998) and Wood Thrushes (see Robbins et al. 1989, Kilgo et al. 1998) appeared to select habitat on broader landscape scales than we expected, and Acadian Flycatchers appeared to select habitat on finer (Kilgo et al. 1998) instead of broader (Robbins et al. 1989, DeGraff and Rappole 1995) scales. Our results provided insights into scales of habitat selection for species for which little information on scale is known: we found that Swainson's Warblers and Yellow-breasted Chats appeared to be associated with broad landscape scales, whereas Prothonotary Warblers appeared to be associated with quite fine scales.

Contrary to our hypotheses, mean scale of landscape variables among bird species was unrelated to successional class, migratory status, or degree of habitat specialization. This suggests that the scale at which a bird perceives habitat, at least in a landscape context, is a function of its unique natural history, perhaps an emergent property of the environmental parameters that define its niche. Therefore, we conclude it is unlikely that any single scale can be used to assess landscape characteristics for any coarse ecological groupings of bird species (much less all birds). This calls into question relationships that are often assumed between forest interior species and area sensitivity (see Villard 1998). Our results indicate that some forest interior species (e.g., Acadian Flycatcher, Ovenbird, American Redstart, Kentucky Warbler) respond to landscapes on fine scales, and therefore may be less sensitive to area constraints than others (e.g., Black-and-white Warbler, Swainson's Warbler, Wood Thrush). Further, although interior species of mature forests are most commonly

associated with area sensitivity, our results suggest that early successional species such as Prairie Warblers and Yellow-breasted Chats respond to landscapes on broad scales; the extent of contiguous early-successional habitat may be limiting for these species, rendering them area sensitive as well.

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